Tooth microwear in *Homo habilis* at olduvai

Preface

The year 1859 is traditionally regarded as the birth of prehistoric researches owing to the excavations at St. Acheul (France) carried out by J.Boucher de Perthes. My grandfather resided at St Acheul and I knew prehistoric stone tools of the Acheulean because they were often placed by the living people of the place on they salon mantelpiece. These are the reasons why in 1959, the announcement by Louis B. Leakey of the discovery at Olduvai Gorge (Tanzania) of an ape-man skull, that was the "connecting link between the South African .near-men and true man .. as we know him", could only strengthen my vocation for Prehistory.

Dating to 1.75 mya, the skull of this robust australopithecine convinced the world that East Africa had been the earliest theatre of human evolution. Mary Leakey discovered the well-preserved cranium initially named *Zinjanthropus boisei,* but later placed in the species *Paranthropus boisei*. This megadont cranium (with absolutely and relatively very large postcanine tooth crowns), assigned OH5 as the fifth honinin discovered at Olduvai, had no mandibles maching until 1964 when a robust-bodied one with postcanine megadontia was recovered from a site on the shore of Lake Natron (80 km west from Olduvai Gorge. The mandible official accession number is NMT-W64-160, but it is universally referred to as Peninj1.

Paranthropus boisei developed an enormous jaw with massive chewing muscles and huge back teeth to help him grind down these tough plant foods. Indeed, many australopithecines and hominines share some sort of feeding specialization that change the dynamics or behaviour as a whole. Each diet or feeding technique is associated with costs and benefits and the following questions can be posed: To what extent would patterns of tooth wear vary in species raised on diets from the same general open environment and so identical in many respects?

Here, we use the dental microwear of two hominin species and a paleoenvironmental approach from Olduvai to contribute to a better understanding of food acquisition by two different species: Homo habilis and Paranthropus boisei

.

Zinjanthropus 

31

Tooth Microwear in *Homo habilis* at Olduvai

P.-F. PUECH

ABSTRACT

The Olduvai *Homo habilis* fossils are the early representatives of the genus *Homo*, two million years ago. They lived side by side with another hominid species: *Australopithecus boisei*. From similar tooth wear patterns of extant species, microscopic observations reveal persuasive evidence of food choice for both *H. habilis* and *A. boisei*. The distinctive features of *H. habilis* are few abrasive alterations, fatigue and erosive wear associated with a specific incisal wear giving evidence of separation of Cyperaceae and/or Gramineae food. In contrast, *A. boisei* is characterized by fatigue and friction wear and more damaged enamel by abrasive grains. It is supposed that the roots of vegetables caused more grit to be eaten. On the incisors' labial enamel of both species we have not noticed the deep gashes which in some later hominids are related to a specific feeding adaptation.

RÉSUMÉ

Les *Homo habilis* fossiles d'Olduvai font partie des premiers représentants du genre *Homo* et datent de deux millions d'années. Ils vivaient côte-à-côte avec une autre espèce d'hominidé, *Australopithecus boisei*. Le choix alimentaire de ces hominidés peut être déduit de la comparaison des aspects de l'usure des dents avec ceux d'hommes et d'animaux actuels. Les traits distinctifs de l'usure des dents d'*Homo habilis* consistent en de rares traces d'abrasion, en une usure par fatigue et par érosion ainsi qu'en un type particulier d'usure des incisives qui témoigne de la sélection par cette espèce d'une nourriture à base de Cypéracées et/ou de Graminées. Les dents d'*Australopithecus boisei* sont caractérisées par une usure par fatigue et friction ; de plus l'émail est davantage altéré par les matières abrasives ; ces particules abrasives sont supposées provenir des racines des végétaux. L'émail labial des incisives des deux espèces ne montre pas les profondes balafres qui, chez certains hominidés plus tardifs, correspondent à une adaptation alimentaire particulière.

In: Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology, Paris 1986, Russell D. E., Santoro J.-P. & Sigogneau-Russell D., Eds, *Mém. Mus. natn. Hist. nat., Paris,* (série C) **53** : 399-414.

Paris, ISBN 2-85653-148-2

Introduction

The type series of specimens for the species *Homo habilis*, representing the first appearance of *Homo* two million years ago, was discovered in northern Tanzania at Olduvai (Leakey *et al.*, 1964). At Olduvai, side by side with *Homo*, also lived the hominid species *Australopithecus boisei.*

Research on variation in early hominids and on the cultural nature of hominid adaptation shows that the close affinities of the two species warrant the comprehensive studies made of their dental adaptations related to diet (Robinson, 1956; Peters, 1981; Puech *et al.*, 1983a). *Homo* developed large incisors which had a better resistance to wear and/or for more incisal preparation, as inferred from similar adaptation in frugivores (Hylander, 1975; Kay, 1977, 1984). In contrast, *A. boisei* has reduced incisor size probably to allow more room for hyper-enlarged-premolars and molars, a dental adjustement related to a savanna habitat (Jolly, 1970). However there are common adaptations in the two species, both having enlarged postcanine teeth that are covered with thick enamel.

The hypotheses of early hominid diet based on analyses of the angulation of occlusal wear facets of the cheek teeth and quantitative analyses of the features of wear are of no use in a comparative study of *Australopithecus* and *Homo* because of morphological variations in the masticatory complex. Therefore in order to discriminate possible dietary categories reflected in tooth wear, we present a microscopic analysis of the dental crowns in *H. habilis* and *A. boisei.* The purpose of this study is only to describe the specific features of wear and not to compare wear facets, so these observations will not deal with the pattern of wear itself.

Material and Method

The initial *H. habilis*, Olduvai Hominid 7 (O.H.7), includes a fragmentary skull with a juvenile mandible estimated to have been 10 years old. The second specimen, O.H.13, a partial skull with a complete dentition, has tooth crowns somewhat damaged by post-mortem erosion so that microscopic analysis is not possible. The third habiline, O.H.16, nicknamed " Olduvai George ", was severely fragmented when it was unearthed. It represents the rare early hominid with matching upper and lower dentitions. The *A. boisei* material is comprised of O.H.5 "Zinjanthropus ", recovered by Mary Leakey in 1959 (Leakey, 1959; Tobias, 1967), and the Peninj mandible from the lower parts of the Ileret sequence 50 miles north-east of Olduvai Gorge (Leakey & Leakey, 1964), two specimens falling within the Olduvai normal magnetic event (1.6-1.9 m.y.) such as O.H.7 and O.H.16 from Olduvai Bed 1 and lower part of Bed 2 (Fig. 1).

The teeth examined were carefully cleaned with acetone in order to eliminate dust particles. Then a nitrocellular impression was made with varnish that provides planar portions of curved surfaces. The choice of a nitrocellular varnish is made to allow observation by photonic transmitted light and scanning. Negative impression provides necessarily more details and less artifacts than duplication with a two step replication. Wear traces are observed under magnifications from 10 to 500 using the techniques described by Puech (1980).

Results

A. *Dental wear*

In *H. habilis* and *A. boisei* the abrasion of teeth produces smooth occlusal surfaces and provides evidence of a rapid rate of dental wear. Theoretically such wear reflects consumption of food that requires high occlusal stress. The large habiline male, O.H.16, shows exposed dentine on every tooth before the third molar erupted into occlusal position, and the lower teeth occluded mesially to their normal position with their maxillary homologues. The edge-to-edge occlusion of the front teeth seems to have been the type of occlusion in Olduvai hominids producing horizontal occlusal wear in the incisors such as present in O.H.5 (Fig. 2), O.H.7 and O.H.16. No crowding of the front teeth is evident for *H. habilis* but *A. boisei* from Peninj presents a slight crowding (Fig. 3).

The microscopic examination of the appar-

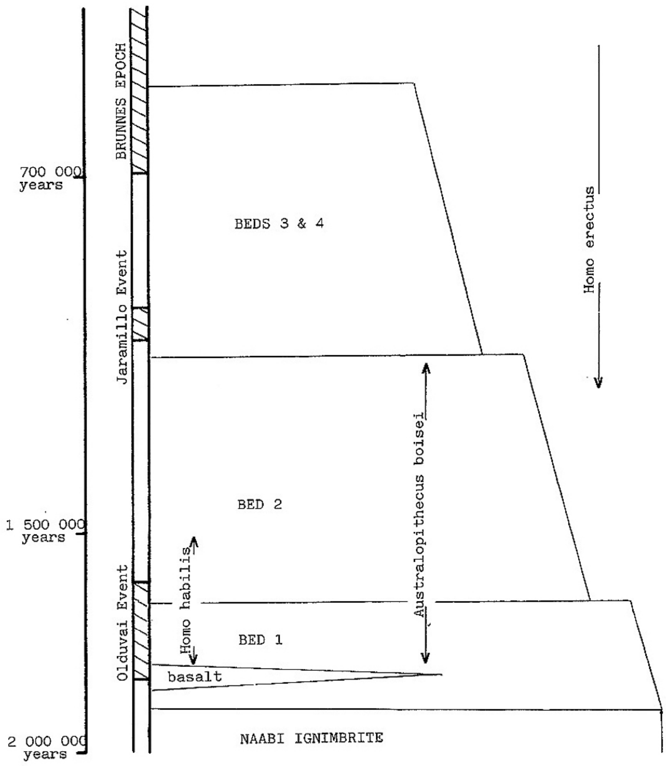


FIG. 1. — Early hominids at Olduvai Gorge (Tanzania): time scale, magnetic epochs and stratigraphic beds.

FIG. 2. — Smooth flat occlusal wear with rounded borders in *Australopithecus boisei* Olduvai Hominid 5 (Courtesy of P. V. Tobias).

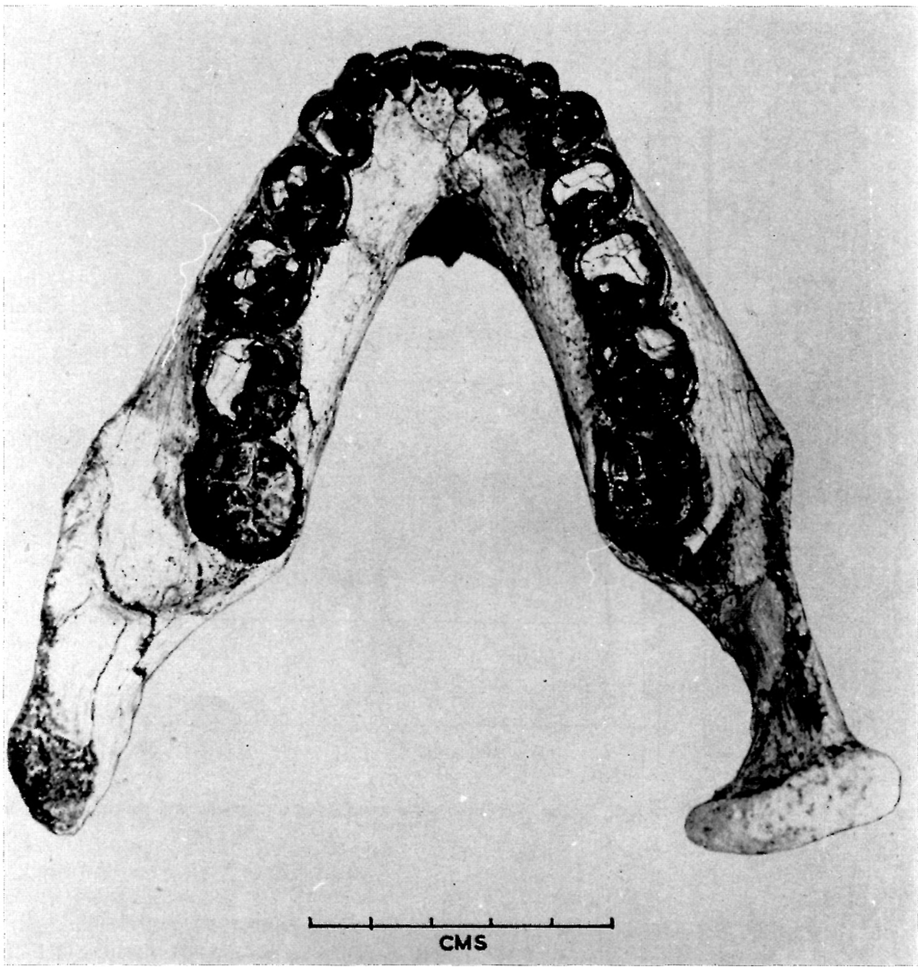


FIG. 3. — *Australopithecus boisei* from Peninj presents a slight anterior dental crowding (Courtesy of P. V. Tobias).

ently smooth aspect of *H. habilis* dental surfaces, gives evidence of patinated enamel bringing the underlying structures into relief in places so that at high magnification a punch-board texture, enamel rods and Hunter-Schreger bands are apparent. Cheek teeth are poorly striated as a consequence of food containing little detritic material or having been washed (Fig. 4). Among apes, poorly striated teeth result from a lack of interest for dusty underground food (Walker, 1976). Eskimos also present fine scratches and abundant small fatigue pits. From these parallels, it is probable that the punch-board texture in *H. habilis* results from a powerful crushing.

Buccal and labial sides of the occlusal surfaces of the teeth of *H. habilis* reveal striae and grooves predominantly bucco- or labio-lingual by oriented. This wear pattern seems to result from " scraping ", " stripping " or " shearing " items. Under higher magnification, the grooves are

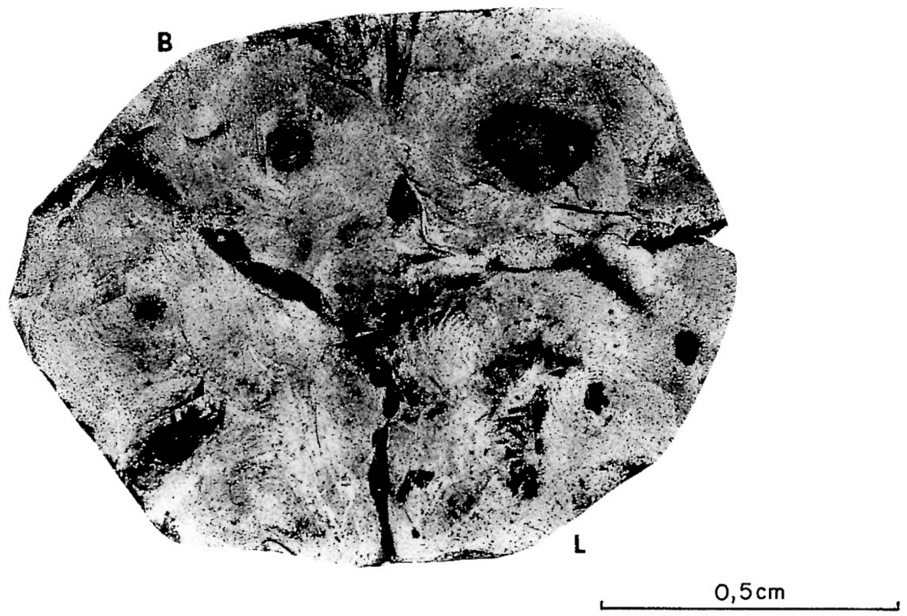


FIG. 4. — Negative cast of the Olduvai Hominid 7 first lower right molar occlusal surface. The distinctive features are very few abrasive alterations with an etched and patinated enamel and dentine.
B = buccal; L = lingual.

almost parallel and of approximately uniform diameter and spacing (Fig. 5). The slight elevations seem to be smoothly polished and the depressions come from chemical etching (Fig. 6). This pattern indicates a process of wear involving the combination of physical and chemical activities of vegetarian origin, since the same fabric-like " furrows " are common in animals eating herbage and swampy plants. Occlusal enamel of the cheek teeth of sheep have a " furrowed " pattern in relation with the enamel prisms arrangement. This pattern can only result from the mastication of Gramineae. These plants contain a siliceous skeleton of opal phytoliths; this amorphous silica is responsible for the parallel scratches varying in width from 0.2-1 μm in mammalian teeth (Walker *et al.*, 1978). These fine parallel scratches can be confused with scratches produced by the exogenous grit adhering to plants (Covert & Kay, 1981) but in many cases microscopic examination allows detection of the origin.

In ancient Egyptian teeth, for example, "furrows " different from scratches (Fig. 7) have been attributed to perennial plants, *Cyperus papyrus*, which grows on the marshy banks of the Nile (Puech *et al.*, 1983b). Phytoliths in the Cyperean family appear as silica situated at the bottom of cells, their apex pointing towards the exterior walls. The phytolith cone, about 8 μm thick, are rarely solitary but grouped in a cluster composed of a variable number. Ancient Egyptians ate young shoots of *Cyperus papyrus* and we suppose that early man did the same with swampy plants. Under a pressure of 10 kg, twice the amount necessary for the structural breakage of the stem of *Cyperus*, the striation produced on enamel in experimental studies is about one twentieth of the width of the abrasive particle (Puech & Prone, 1979). The striations produced by phytoliths should then be 0.4 μm wide, close to the mean value of the " scratches " produced by grass on enamel (Walker *et al.*, 1978).

The characteristics of the " furrows " are probably the result of a multiplicity of factors occurring during the mastication of plant tissues (Rensberger, 1978). An explanation of the physi-

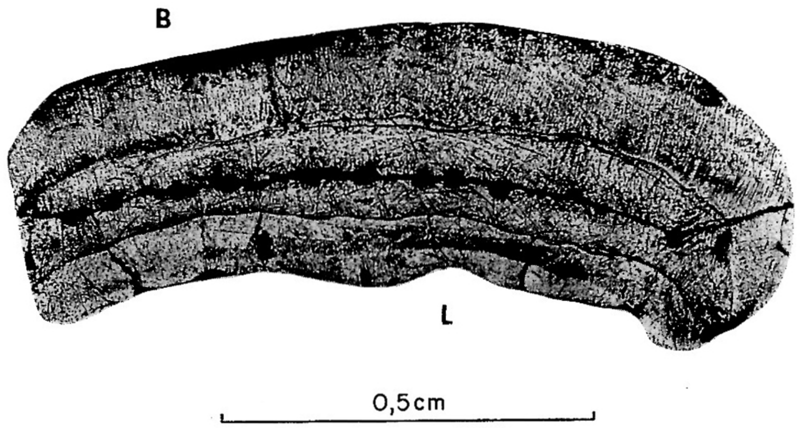


FIG. 5. — Central upper right incisor of Olduvai Hominid 16. The occlusal surface gives evidence of a specific incisal use by labio-lingually oriented furrows and striae.
B = buccal; L = lingual.

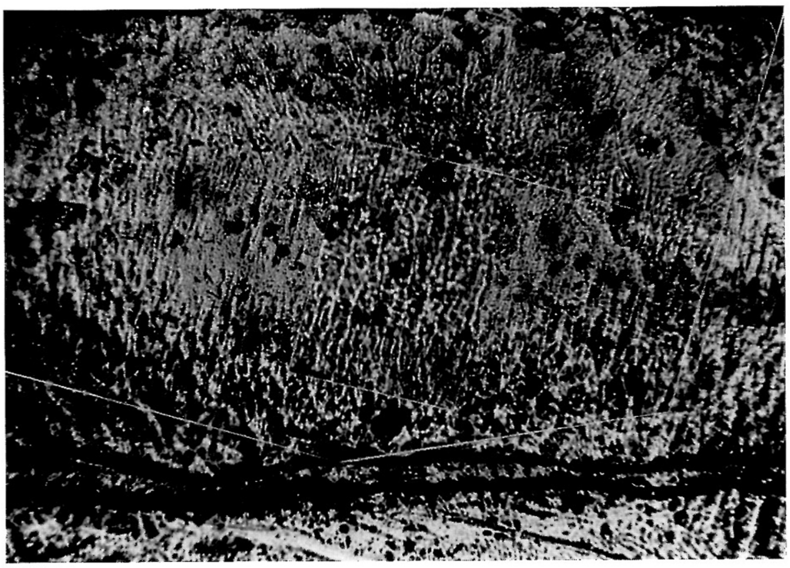


FIG. 6. — Central incisal surface of the central upper right incisor of Olduvai Hominid 16, × 50. The furrows running from the enamel-dentine junction are almost parallel and of uniform diameter and spacing.

FIG. 7. — Furrows in ancient Egyptian teeth — upper left of the figure — are attributed to a wear process involving mastication of Cyperaceae. × 50.

cal and chemical events leading to the production of " furrows " has already been proposed (Puech, in press). Based on the polishing resulting from the friction of food and on the granulometric distribution of phytolith particles, Cyperaceae and Graminae produce the characteristically blunt appearance of wear associated with fine " striae " (Fig. 8).

The erosive action of the diet of *H. habilis* from Olduvai is confirmed by a burnished appearance of the second upper molars in O.H.16. These second molars showed localised hypoplasia and erosion that were the result of chewing habits (Tobias, 1976). The same pattern of erosion has recently been noted in extant human juveniles who chew aspirin for the relief of rheumatoid arthritis (Sullivan & Kramer, 1983), and thus Puech (1984) related the burnished appearance seen in O.H.16 with the injurious effects of chewing resistant acidic material (Fig. 9).

Hypoplasia of the enamel is a common feature in Olduvai hominids. The type specimens of *A. boisei* (Fig. 10) and *H. habilis* (Fig. 11), namely O.H.5 and O.H.7, were affected. From the levels of strips of hypoplastic enamel in O.H.5, Tobias (1974) concluded that the *A. boisei* youth had

FIG. 8. — Blunt appearance of the furrows present in the lateral lower incisor of Olduvai Hominid 16, × 500. Central labial margin of the occlusal surface.

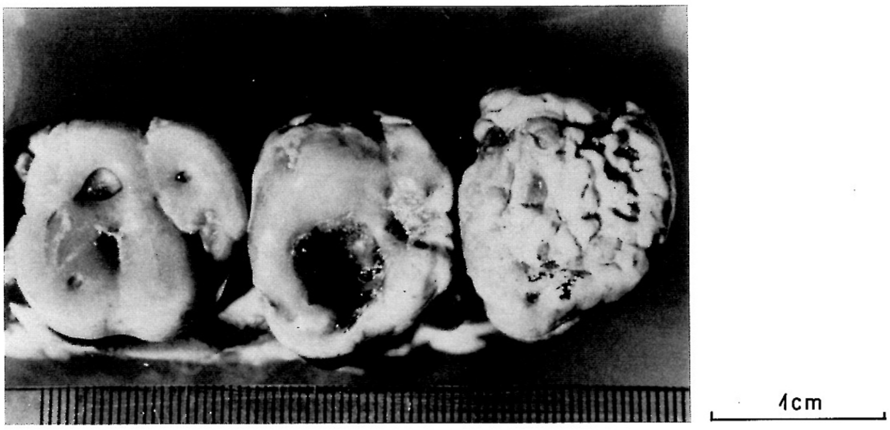


FIG. 9. — Burnished second upper right molar in Olduvai Hominid 16 and the localized erosion attributed to the chewing of resistant acidic vegetables (Courtesy of P. V. Tobias).

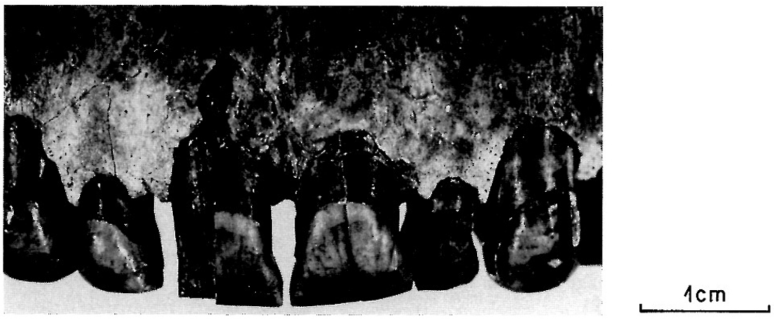


FIG. 10. — Hypoplasic grooves and pits on the labial enamel in Olduvai Hominid 5 (Courtesy of P. V. Tobias).

been subject to systemic upsets. Hypoplasia and acidic food acted in combination producing the concave erosion that occurs on the second molars of O.H.16. Food accumulated in the major occlusal pit, and because the enamel there was thinner and hypoplasied, the topical effect was most injurious.

In contrast, *A. boisei* fed on more dusty material that has produced smooth, flat occlusal wear with rounded borders. Microscopically, the teeth of *A. boisei* appear to have been damaged by abrasive grains; the latter moreover produced micro-pits in the incisor enamel during grasping action, and deeply striated the posterior teeth during the grinding of food (Figs. 12 and 13). Furthermore the occlusal margins of the interstitial surfaces are frequently irregular and polished, suggesting that microscopic irregularities of the surface are caused by enamel fatigue and abrasive material. Foraging habits in the Chacma baboon includes extraction of belowground vegetables; our analysis of dental microwear shows a similar abrasive grain action. In consequence, we accept the thesis of the use of an earth-digging stick as being responsible for the high percentage of abrasive particles that have worn down *A. boisei* teeth, producing smooth rounded occlusal borders and a deeply recessed dentine. Con-

FIG. 11. — Hypoplasia (central dark region) and absence of deep grooves on labial enamel of the central lower right incisor of Olduvai Hominid 7, × 50. Occlusal surface at top.

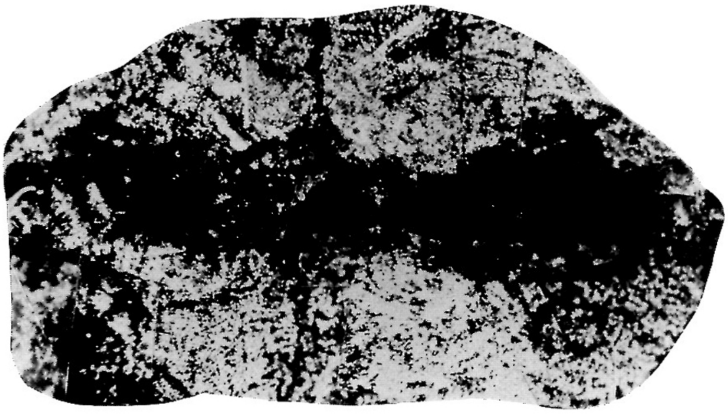
sumption of belowground plants in combination with food having a high friction action, associated with heavy mastication, seems to be responsible for hyper-enlarged cheek teeth.

In the front teeth, striations result from the movement of mandibular teeth during ingestion and mastication as well as from the use of the hands to hold, pull or push food and other objects. In *H. habilis* and *A. boisei*, incisal dentine presents large mesio-distal striae produced by a slicing action. On the labial surfaces no additional deep grooves have been observed. These grooves in monkey (*Papio ursinus*) and later hominids (*H. erectus* and *H. sapiens*) come from the common use of front teeth to assist the hands.

B. *Habitat*

The *H. habilis* and *A. boisei* remains at Olduvai and Peninj were discovered in alluvial and lacustrine sedimentary deposits interbedded with volcanic aeolian tuffs. The length of the sequence in which *H. habilis* was recovered together with *A. boisei* shows that apparently no niche divergence occurred.

The fossil Olduvai fauna (that closely resembles the extant fauna), as well as palaeobotanical information, indicate the persistence of wooded grassland and of an acacia savanna environment in early hominid-bearing sediments (Bonnefille, 1985; Denys, 1985; Jaeger, 1976, 1979; Leakey, 1965; Petter, 1973; Rage, 1973). Palaeoecological reconstruction of the way of life of early homin-



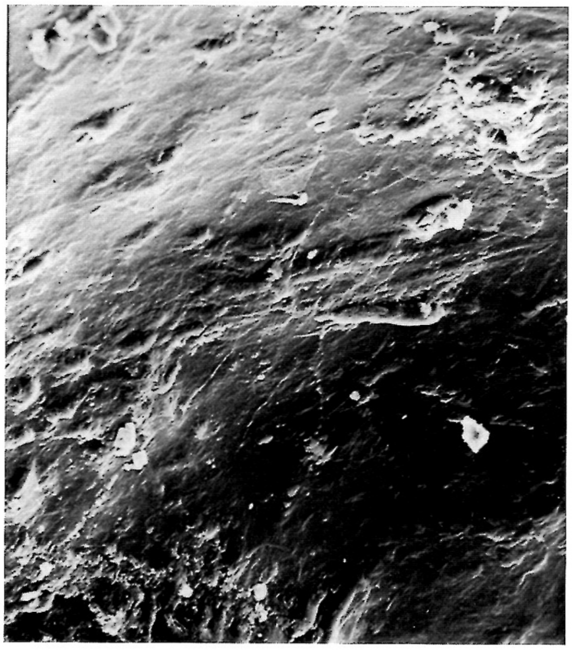


FIG. 12. — Damaged occlusal surface of a lateral lower incisor in *Australopithecus boisei* at Peninj, low (× 30) and higher (× 300) magnification. Labial surface down.

FIG. 13. — Polished occlusal enamel with many striations in the second lower left premolar of the Peninj mandibule. Striations running from buccal, at left, to lingual surface at magnification of 50.

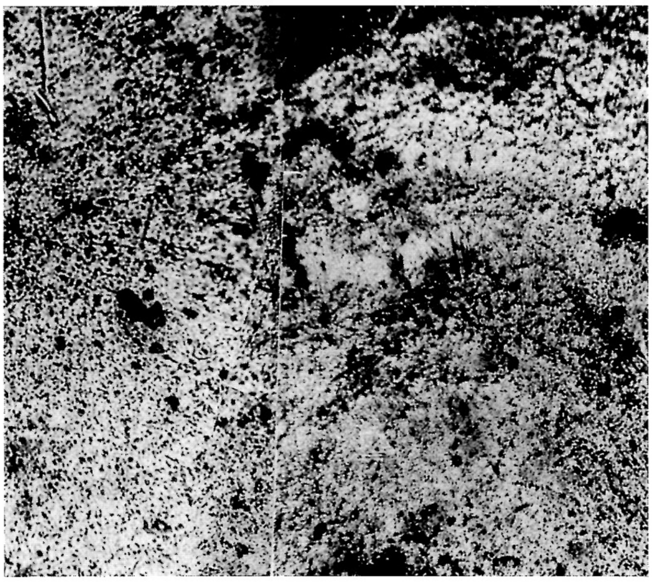


FIG. 14. — Etched occlusal enamel of the first lower right molar of Olduvai Hominid 7. Detail × 50 from Fig. 4.

ids at Olduvai testify to a lake margin or flood plain setting (Hay, 1976). Swampy vegetation is indicated by vertical non-branching root casts, and marshland by identification of *Cyperus papyrus*. *Cyperus papyrus* and other *Cyperus* species have a particular nutritional richness (Hatley & Kappelman, 1980).

Savanna type habitat and lake margins are characterized by vegetable species that produce nut-like fruits, legumes, tubers, rhizomes, roots and stem bases of water-edge plants. Thus, basically, sources of vegetable food for omnivore hominids were diversified. Furthermore stone tools associated with animal bone remains imply a meat-eating habit by Olduvai *H. habilis*. Apparently the decisive factors of food choice must have been seasonal and annual availability as well as qualitative composition of the food.

Discussion and Conclusion

In monkeys the use of incisors varies according to the species, even if they process similar food. Walker (1976) presented observations giving evidence that *Papio* used incisors to process lettuce twice as much as did *Colobus*. The absence of deep grooves on the labial faces of the front teeth in *H. habilis* and *A. boisei* may, as well, not be exclusively due to the absence of special mechanical demands.

Molar microwear provides a good guide for detecting food choice since cheek teeth have the sole function of grinding food before swallowing. However no microwear feature can be exclusively attributed to bone-crushing or to scraping and slicing meat because in carnivorous mammals teeth have a polished enamel that is inconclusive for hominids (Puech, 1980). Evidence of meat eating in *Homo* is therefore to be searched for rather in detailed studies of stone artefacts and in cut-marks on bones.

On microscopic examination the molar teeth of *H. habilis* from Bed 1 and Bed 2 at Olduvai reveal evidence of enamel and dentine erosion (Figs. 14 and 16). The erosion affecting all crown surfaces and accelerating tooth wear results in a typical microscopic appearance. From this it would appear that the Olduvai habilines chose acidic food. Ripe fruits are a dietary staple for apes. In some areas, however, orang utans and chimpanzee specialize seasonally on unripe fruits (Fig. 15) (Galdikas, 1982; Nishida *et al.*, 1983) and Chacma baboons eat bitter fruits rejected by birds. Like the Chacma baboon (Hamilton *et al.*, 1978a), *H. habilis* may have selected the immature stages of most vegetation and some fruits to reduce the cellulose content and to secure fruits before other animals could feed on them.

Cyperaceae, with a particularly high mineral content in the form of phytoliths, have produced a characteristic pattern in the incisives of *H. habilis* (Fig. 17). *Cyperus* was available to *Homo* and *Australopithecus*, but Hamilton *et al.* (1978b) report that *Cyperus* root-processing observed in baboons does not occur in other animals because it needs manual dexterity to separate the protective sheaths from the bulbs and stems. Cyperaceae from swamp margins and river banks is a starchy food that could have been sufficient for the energetic needs of early man, but its consumption is a time-consuming habit only adopted in ancient Egyptians when a decline in alternative resource was occurring. Comparative microwear analyses, ethnological and palaeoecological documentation are thus providing evidence of acidic swampy vegetable feeding by *H. habilis* at Olduvai.

variety of food items and only some of these items produced the features described in the present study. It is also evident that some features are related to differences in occlusal forces that can be inferred from the morphology of the masticatory systems (Rak, 1985). However, microwear gives evidence that the two hominid species at Olduvai, *A. boisei* and *H. habilis*, had a divergent food choice. Together with a time-table concerning the occupation of water holes, different food choice may explain the synchronism that does not necessarily mean a common life. Comparison of techniques of food processing shows variations between chimpanzee populations. Some ignore the nuts, others only eat the outer energy-rich husk and others use stone tools to extract the protein-rich kernel (McGrew, 1986).

We can imagine *H. habilis* settling in a territory already inhabited by *A. boisei*. Rather than exterminating *A. boisei*, *Homo* would have used him as a vanguard. This arrangement may be a good example of opportunism by our ancestors and explain the extinction of *A. boisei* and the success of *Homo* as a consequence of the variability of early hominid behavior in a same environment.

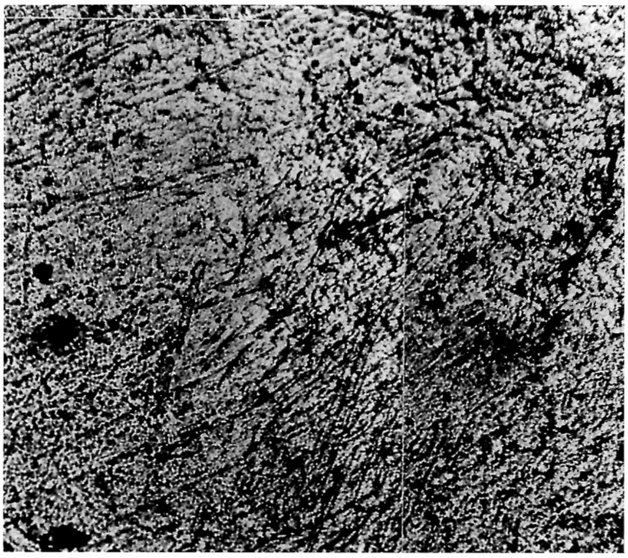


FIG. 15. — Etched enamel is observed in *Pongo* after unripe fruit action. Buccal side of the occlusal enamel of a lower right first molar × 50.

FIG. 16. — Buccal surface of the first right lower molar of Olduvai Hominid 7, occlusal margin at top. Magnification 50 gives evidence that all crown surfaces are eroded.

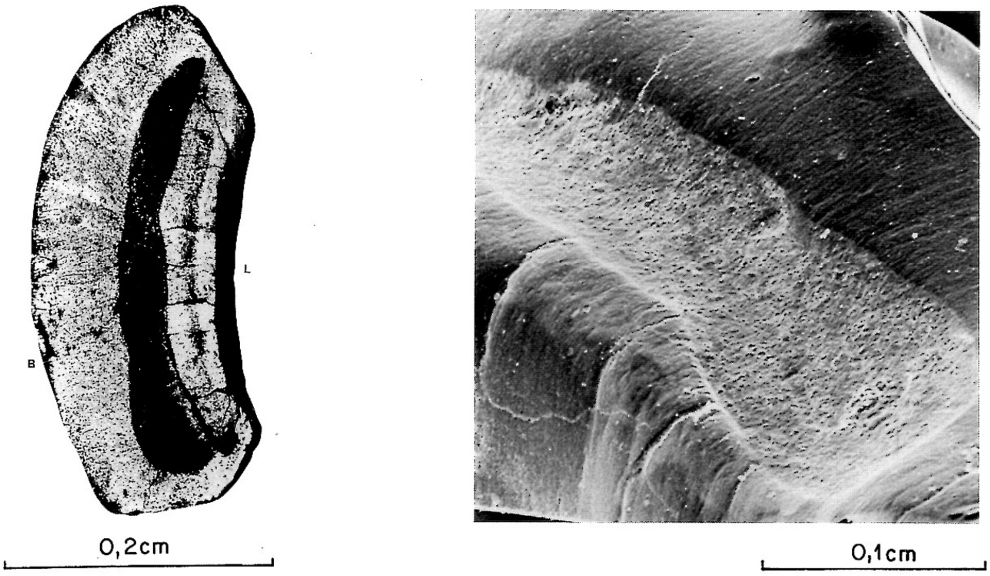


FIG. 17. — Photonic transmitted light and scanning observation of the characteristic wear pattern in front teeth of *Homo habilis* at Olduvai. Olduvai Hominid 7 central lower right incisor.
B = buccal; L = lingual.

ACKNOWLEDGEMENTS

This work formed part of a lecture presented to the Collège de France, séminaire " Paléoanthropologie et Préhistoire " du Pr. Yves Coppens 1985/86.

We wish to thank Yves Coppens, Mary Leakey, Richard Leakey, Phillis Leek, Henry de Lumley, Marie-Antoinette de Lumley, Phillip V. Tobias and Hervé Tyrand for their help and assistance.

REFERENCES

BONNEFILLE R., 1985. — Evolution of the continental vegetation: the palaeobotanical record from East Africa. *S. Afr. J. Sci.*, **81**: 267-270.

COVERT H. H. & KAY R. F., 1981. — Dental microwear and diet: implications for determining the feeding behaviours of extinct primates, with a comment on the dietary pattern of *Sivapithecus*. *Am. J. Phys. Anthrop.*, **55**: 331-336.

DENYS C., 1985. — Palaeoenvironmental and palaeobiogeographical significance of the fossil rodent assemblages of Laetoli (Pliocene, Tanzania). *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **52**: 77-97.

GALDIKAS B. M. F., 1982. — Orang utans as seed dispersers at Tanjung Puting, central Kalimantan: implications for conservation. *In: The Orang utan, its biology and conservation*, de Boer L. E. M., Ed., D. W. Junk, The Hague.

HAMILTON W. J., BUSKIRK R. E. & BUSKIRK W. H., 1978a. — Environmental determinants of object manipulation in Chacma baboons (*Papio ursinus*) in two southern African environments. *J. Hum. Evol.*, **7**: 205-216.

HAMILTON W. J., BUSKIRK R. E. & BUSKIRK W. H., 1978b. — Omnivory and utilization of food resources by Chacma baboons, *Papio ursinus. The American Naturalist*, **112** (987): 911-924.

HATLEY T. & KAPPELMAN J., 1980. — Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of belowground food resources. *Hum. Ecol.*, **8**: 371-387.

HAY R. L., 1976. — Environmental settings of hominid activities at Bed 1 Olduvai. *In: Human origins, Louis Leakey and the East African evidence*, Isaac G. L. & Mc Cown E. R., Eds., W. A. Benjamin, Menlo Park, Calif: 209-225.

HYLANDER W. L., 1975. — Incisor size and diet in anthropoids with special reference to Cercopithecidae. *Science*, **189**: 1095-1098.

JAEGER J. J., 1976. — Les rongeurs (Mammalia, Rodentia) du Pleistocène inférieur d'Olduvai Bed 1 (Tanzanie), I[ere] partie : les Muridés. *In: Fossil vertebrates of Africa*, vol. 4, Savage R. J. G. & Coryndon S. C., Eds., Academic Press, New-York: 58-120.

JAEGER J. J., 1979. — Les faunes de rongeurs et lagomorphes du Pliocène et du Pleistocène d'Afrique Orientale. *Bull. Soc. Geol. Fr.* 7[e] sér., **21**: 301-308.

JOLLY C. L., 1970. — The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man*, **5**: 5-26.

KAY R. F., 1977. — Diet of early Miocene African hominoids. *Nature*, **268**: 628-630.

KAY R. F., 1984. — On the use of anatomical features to infer foraging behavior in extinct primates. *In: Adaptations for foraging in nonhuman primates*, Rodman P. S. & Gantt J. G. H. Eds., Columbia Univ. Press, New York: 21-53.

LEAKEY L. S. B., 1959. — A new fossil skull from Olduvai. *Nature*, **184**: 491.

LEAKEY L. S. B. & LEAKEY M. D., 1964. — Recent discoveries of fossil hominids in Tanganyika at Olduvai and near Lake Natron. *Nature*, **202**: 5-7.

LEAKEY L. S. B., TOBIAS P. V. & NAPIER J. R., 1964. — A new species of the genus *Homo* from Olduvai Gorge. *Nature*, **202**: 7-9.

LEAKEY L. S. B., 1965. — *Olduvai Gorge*, vol. 1: *Fauna and background*. Cambridge Univ. Press, Cambridge.

MC GREW W. C., 1986. — Chimpanzee material culture. What are its limits and why? *In: The Pleistocene perspective* vol. 1: *The World Archaeological Congress*, Day M. & Foley R., Eds., Allen and Unwin.

NISHIDA T., WRANGHAM R. W., GOODALL J. & UEHARA S., 1983. — Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *J. Hum. Evol.*, **12**: 467-480.

PETERS C. R., 1981. — Robust vs. gracile early hominids masticatory capabilities: the advantages of the megadonts. *Anthrop. UCLA*, **7**: 161-181.

PETTER G., 1973. — Carnivores pleistocènes du ravin d'Olduvai. *In: Fossil Vertebrates of Africa*, Savage R. J. G. & Coryndon S. C., Eds., Academic Press, New York: **3**: 43-100.

PUECH P.-F. & PRONE A., 1979. — Reproduction expérimentale des processus d'usure dentaire par abrasion: implications paléoécologiques chez l'homme fossile. *C. R. Acad. Sc. Paris*, série D, **289**: 895-898.

PUECH P.-F., 1980. — *Les premiers hommes en Eurasie*. Mémoire de D.E.A. Univ. Provence: Marseille.

PUECH P.-F., SERRATRICE C. & LEEK F. F., 1983a. — Tooth wear as observed in ancient Egyptian skulls. *J. Hum. Evol.*, **12**: 617-629.

PUECH P.-F., ALBERTINI H. & SERRATRICE C., 1983b. — Tooth microwear and dietary patterns in early hominids from Laetoli, Hadar and Olduvai. *J. Hum. Evol.*, **12**: 721-729.

PUECH P.-F., 1984. — Acidic-food choice in *Homo habilis* at Olduvai. *Cur. Anthropol.*, **25**: 349-350.

PUECH P.-F., in press. — Dental microwear features as an indicator for plant food in early hominids: a preliminary study of enamel. *Human Evolution.*

RAGE J. C., 1973. — Fossil snakes from Olduvai, Tanzania. *In: Fossil vertebrates of Africa*, **3**, Savage R. J. G. & Coryndon S. C., Eds., Academic Press, New York: 1-6.

RAK Y., 1985. — Australopithecine taxonomy and phylogeny in light of facial morphology. *Am. J. Phys. Anthrop.*, **66**: 281-287.

RENSBERGER J. M., 1978. — Scanning electron microscopy of wear and occlusal events in some small herbivores. *In: Development, Function and Evolution of teeth*, Butler P. M. & Joysey K. A., Eds., Academic Press, London: 415-438.

ROBINSON J. T., 1956. — The dentition of the Australopithecinae. *Transvaal Mus. Mem. (Pretoria)*, **9**.

SULLIVAN R. E. & KRAMER W. S., 1983. — Iatronic erosion of teeth. *J. Dent. Child.*, **50**: 193-196.

TOBIAS P. V., 1967. — *Olduvai Gorge*, vol. 2: *The cranium and maxillary dentition of Australopithecus (Zinjanthropus) boisei*. Oxford Univ. Press, London.

TOBIAS P. V., 1974. — Aspects of pathology and death among early hominids. *The Leech*, **44**: 119-124.

WALKER A., HOECK H. N. & PEREZ L., 1978. — Microwear of mammalian teeth as an indicator of diet. *Science*, **201**: 908-910.

WALKER P L., 1976. — Wear striations on the incisors of cercopithecid monkeys as an index of diet and habitat. *Am. J. Phys. Anthrop.*, **45**: 299-308.